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Abstract: The replacement of the late Precambrian Ediacaran biota by morphologically disparate animals at the beginning of the Phanerozoic was a key event in the history of life on Earth, the mechanisms and the timescales of which are not entirely understood. A composite section in Namibia providing biostratigraphic and chemostratigraphic data bracketed by radiometric dating constrains the Ediacaran–Cambrian boundary to 538.6–538.8 Ma, more than 2 Ma younger than previously assumed. The U–Pb-CA-ID TIMS zircon ages demonstrate an ultrashort time frame for the LAD of the Ediacaran biota to the FAD of a complex, burrowing Phanerozoic biota represented by trace fossils to a 410 ka time window of 538.99±0.21 Ma to 538.58±0.19 Ma. The extremely short duration of the faunal transition from Ediacaran to Cambrian biota within less than 410 ka supports models of ecological cascades that followed the evolutionary breakthrough of increased mobility at the beginning of the Phanerozoic.

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ABSTRACT

The replacement of the late Precambrian Ediacaran biota by morphologically disparate animals at the beginning of the Phanerozoic was a key event in the history of life on Earth, the mechanisms and the timescales of which are not entirely understood. A composite section in Namibia providing biostratigraphic and chemostratigraphic data bracketed by radiometric dating constrains the Ediacaran–Cambrian boundary to 538.6–538.8 Ma, more than 2 Ma younger than previously assumed. The U–Pb-CA-ID TIMS zircon ages demonstrate an ultrashort time frame for the LAD of the Ediacaran biota to the FAD of a complex, burrowing Phanerozoic biota represented by trace fossils to a 410 ka time window of 538.99±0.21 Ma to 538.58±0.19 Ma. The extremely short duration of the faunal transition from Ediacaran to Cambrian biota within less than 410 ka supports models of ecological cascades that followed the evolutionary breakthrough of increased mobility at the beginning of the Phanerozoic.

INTRODUCTION

The replacement of the enigmatic Ediacaran biota by morphologically disparate animals (metazoans) at the beginning of the Phanerozoic was a key event in the history of life, which has been explained by environmental, evolutionary or ecological factors, possibly superimposed by a major taphonomic bias (e.g., Laflamme et al., 2013; Darroch et al., 2015; Schiffbauer et al., 2016;

Muscente et al., 2018). These hypotheses predict different timescales for this turnover; however, age data with sufficient time resolution have been lacking to date. Ediacaran–Cambrian boundary sections on the Swartpunt and Swartkloofberg farms in Southern Namibia (Saylor and Grotzinger, 1996) combine rich palaeontological data (Darroch et al. 2015) with the presence of tuff layers that allow high-precision radio-isotopic age determination. Grotzinger et al. (1995) published pioneering work in dating these tuffs, using multigrain air-abrasion U–Pb on zircon ID-TIMS technique. Their analytical precision was insufficient to quantify the timescale necessary for establishing new metazoans. Here we present new high-precision U–Pb-CA-ID TIMS zircon ages from these tuff layers that provide a much refined age datum for the beginning of the Cambrian and the first absolute ages for the evolutionary transition from the Ediacaran biota to the existence of complex Phanerozoic trace makers.

DEFINITION AND TIME FRAME OF THE EDIACARAN–CAMBRIAN BOUNDARY

The Ediacaran–Cambrian boundary is characterized by the appearance of advanced Eumetazoa (i.e., Bilateria). Evidence is the rather rapid appearance of complex trace fossils, formally defined by the lower boundary of the *Treptichnus pedum* Assemblage Zone in the GSSP at Fortune Head, Newfoundland. There, *T. pedum* appears for the first time (Brasier et al., 1994; Geyer and Landing, 2016), which is otherwise recognizable by the first pronounced bioturbation in earth history (Buatois and Mángano, 2016, Buatois et al., 2018). This concept appears to conflict with bilaterian trace fossils in the Ediacaran (e.g., Chen et al., 2018), albeit considered subhorizontal traces of undermat miners. This boundary was previously noted to occur around 541.00±0.81 Ma (Amthor et al., 2003; Bowring et al., 2007), based on a U–Pb zircon age of an ash sample from the Ara Group of Oman. This ash occurs just below a sequence that records a negative $\delta^{13}C$ isotope excursion termed the Basal Cambrian Carbon Isotope Excursion (BACE) (Zhu et al., 2004) and immediately above strata hosting the biomineralized tubular fossil *Cloudina*. However, biostratigraphic data are completely

lacking from the strata above the ash layer. The GSSP section for the Ediacaran–Cambrian boundary in Avalonian Newfoundland lacks the soft-bodied Ediacaran biota as well as dateable ash beds (Brasier et al., 1994; Geyer and Landing, 2016). From the boundary sections of the Yangtze/South China sequence, the Ediacaran–Cambrian boundary was dated between 542.6±3.7 Ma and 536.3±5.5 Ma (Chen et al., 2015). Ash beds related to this boundary are yet unknown from other relevant sections globally, such as those in the Flinders Ranges (Australia), Siberia, the Ukraine (Brasier et al., 1994), the White Inyo–Death Valley–Mojave regions (California) (Hagadorn et al., 2000) or the Mount Dunfee section (Nevada) (Smith et al., 2016).

NAMIBIAN KEY SECTIONS AND NEW ZIRCON AGES

Sections of the upper Ediacaran Spitskop Member (Urusis Formation, Schwarzrand Group) and the lower Cambrian Nomtsas Formation (Nama Group) are preserved in the Witputs Subbasin of the Nama Basin (Fig. 1) and exposed on Swartpunt and Swartkloofberg farms in southern Namibia (Fig. 2, Saylor and Grotzinger, 1996). These sections are invaluable for studying the development of complex life during the Ediacaran–Cambrian transition as they contain a unique association of ash beds suitable for radiometric dating, carbonates useful for stable isotope chemostratigraphy, and imprints of soft-bodied and biomineralized remains of the Ediacaran biota (Fig. 3). Importantly, this sequence also includes trace fossils indicative of bilaterian metazoans that are significant for biostratigraphic analysis. Recent field studies of these outcrops have resulted in the division of the Swartpunt section into units A–F, whereas the nearby Swartkloofberg section represents a terminal unit G (Figs. 2 and 3). Units A–F comprise a 139 m thick intercalation of limestone, shale and sandstone of the upper Spitskop Member. Rapid regional uplift led to a hiatus in deposition caused by incision of canyons into the Spitskop Member. Sedimentary infilling of these valleys forms unit G of the Nomtsas Formation (Saylor and Grotzinger, 1996).

Ash beds in the Swartpunt and Swartkloofberg sections have been dated at 545.1±1 Ma (middle part of the Spitskop Member, upper Ediacaran), 543.3±1 Ma (Spitskop Member, unit A of this paper) and 539.4±1 Ma (Nomtsas Formation, unit G of this paper) (Grotzinger et al., 1995, Bowring et al., 2007). These ages were recalculated to 542.68±2.8 Ma for the middle part of the Spitskop Member, 540.61±0.67 Ma for the upper part of the Spitskop Member and 538.18±1.11 Ma for the base of the Nomtsas Formation (Schmitz, 2012).

The Ediacaran rangeomorph/erniettomorph biota, including such forms as *Swartpuntia germsi* and *Pteridinium simplex* (Figs. 3, 4A and 6) (Saylor and Grotzinger, 1996; Narbonne et al., 1997, 2012), occur in siliciclastic, storm-dominated shelf deposits of unit D but are absent above metre 107. The Ediacaran–Cambrian transition interval (ECTI, Fig. 3) is represented by an 18 m thick limestone (unit E). Metres 125 to 128 of unit F contain an association of diverse trace fossils, including branched forms such as *Streptichnus narbonnei* (Jensen and Runnegar, 2005) and *Treptichnus* cf. *pedum* (Figs. 3 and 4B–D), and other ichnofossils of Fortunian and Phanerozoic aspect (Fig. 4–J). A recent study also emphasizes the presence of trace fossils produced by sediment bulldozers in this part of the section, which "may in fact be regarded as a representative of Cambrian-style bioturbation" (Buatois et al., 2018, p. 3). Simple, Ediacaran-type traces are represented by *Helminthopsis*, which are also known from older strata of the Huns Member and the Nudaus Formation, as are the non- or poorly mineralized body fossils *Gaojiashania* and *Shaanxilithes* (Darroch et al., 2016; Smith et al., 2017). These fossil assemblages indicate a progressive rise of more complex organisms, peaked by the advent of complex and burrowing metazoans responsible for the successive reduction in the extent of microbial mats above a 547.36±0.23 Ma old ash (Bowring at al., 2007). The trace fossil interval is overlain by a black, thin-bedded micrite with biomineralized Ediacaran taxa such as *Cloudina* and *Namacalathus*.

The trace fossil assemblage in the 3 m thick unit F in the Swartpunt section marks the emergence of Cambrian (and Phanerozoic-type) advanced bilaterians, represented by *Streptichnus narbonnei* and *Treptichnus* cf. *pedum*. *Streptichnus narbonnei* reflects the complex behaviour of its producer, which corresponds to that displayed by *Treptichnus pedum*. Specimens assigned to *T. pedum* from the younger, Terreneuvian, Rosenhof Member of the Fish River Subgroup (Geyer and Uchman, 1995) show a transition between the two ichnospecies. The rather sudden appearance of complex traces in the Ediacaran–Cambrian boundary section at the GSSP in Newfoundland (Geyer and Landing, 2016), therefore, matches a similar appearance of such traces with Phanerozoic aspect in the Namibian sections (Fig. 4E–J), where the lowest occurrence of *T.* cf. *pedum* is in unit F (Figs. 3 and 4D).

In the Swartpunt section (Fig. 3), ash beds crop out as 8 to 80 cm thick, whitish-greenish, splintery, silicified and weathering-resistant layers. U–Pb age determinations were performed applying CA-ID-TIMS to zircon grains, using the EARTHTIME ^{205}Pb–^{233}U–^{235}U tracer solution (ET 535, http://www.earthtime.org) (for methods and data table see Supplementary Data, SD Table 1; the results are presented in Fig. 5). Ash 1, located in unit A, has yielded an age of 540.095±0.099 Ma. Up-section in unit C in ascending stratigraphic order, ashes 2 to 5 have depositional ages of 539.58±0.34 Ma, 539.52±0.14 Ma, 539.64±0.19 Ma and 538.99±0.21 Ma. In unit G of the lower Nomtsas Formation, the 25 cm thick ash 6 (538.58±0.19 Ma) exhibits features similar to those of older ashes and has been ripped into metre-sized fragments. Due to the wide distribution of related fragments over several decametres, we assume ash 6 is a primary ash bed in the Nomtsas Formation, which has been fragmented during sediment deposition. Alternatively and less probable, ash 6 could be reworked material from the underlying Spitskop Member. If so, its age of 538.58±0.19 Ma provides a maximum depositional age of the Nomtsas Formation. In any case, this age provides a minimum age for the base of the Cambrian. Even if ash 6 occurred primary in the Spitskop Member, it must be younger than ash 5 (538.99±0.21 Ma) and also younger than the Cambrian fossil-bearing bed in unit F, because no additional ash bed exists between ash 5 and the Cambrian fossil assemblage at metre

127 of the Swartpunt section. It should be noted that another ash bed aged 538.18±1.11 Ma is reported from unit G in the Nomtsas Formation (Grotzinger et al., 1995, recalculated by Schmitz, 2012).

Slight positive uniform $\delta^{13}C$ ratios around +1 (Fig. 3, SD Table 3), combined with biostratigraphic constraints, place units A–F into the range of the late Ediacaran Positive Carbon Isotope Plateau (EPIP) and seemingly below the BACE, according to Zhu et al. (2017). The BACE does not occur in the section (Fig. 3). Reasons could be (i) a shallow bathymetry of the section, (ii) that the BACE is possibly not global, or (iii) the Ediacaran–Cambrian boundary, at least in the Swartpunt section, is far below the BACE. However, the age determinations suggest that units A–F lie well above the strong positive $\delta^{13}C$ excursion detected in the Ara Group of Oman (Amthor et al., 2003). Similarly, *S. narbonnei* and *T. pedum*, indicative for Cambrian age as produced by advanced bilaterians, occur in all known sections above the BACE, but reliable changes in trace fossil assemblages that are believed to be indicative of phylogenetic changes are only known from the Fortune Head section and the sections presented here.

IMPLICATIONS FOR THE TIMING AND NATURE OF BIOTIC CHANGES

The stratigraphic sequence at Swartpunt confirms that the disappearance of rangeomorphs and erniettomorphs was rapidly followed by the advent of complex bilaterian trace-makers, and demonstrates that Ediacaran biomineralized taxa extended for a short time beyond this key event, at least locally.

Our new age data provide for the first time a precise, absolute timing for this evolutionary turnover during the Ediacaran–Cambrian transition (Fig. 6). Accordingly, the age of ash 5 (538.99±0.21 Ma) predates the termination of the erniettomorph *Pteridinium simplex* and rangeomorph *Swartpuntia germsi* in unit D at metre 104. The first appearance of Cambrian-type

ecosystem indicators, including *Streptichnus narbonnei*, can now be dated at between 538.99±0.21 Ma (ash 5) and 538.58±0.19 Ma (ash 6). Thus, the extinction of the rangeomorphs/erniettomorphs and the beginning of the Cambrian radiation occurred within a short period of 410 ± 400 ka, given by the age difference between ashes 5 and 6. It should be noted that this duration is overestimated, because it includes an erosional unconformity in the basal Cambrian (Fig. 3). Furthermore, ash 6 predates the first appearance of *Treptichnus pedum*, part of a moderately diverse assemblage. We therefore suggest the age of the Ediacaran–Cambrian boundary between ash 5 and ash 6 needs to be ca. 538.8 Ma, thus about ca. 2.4 Ma younger than previously suggested.

The new timeframe allows testing of different evolutionary models for the replacement of the Ediacaran-type biota (ETB) by the Cambrian-type fauna (CTF) (Laflamme et al., 2014; Darroch et al., 2015; Smith et al., 2016; Muscente et al., 2018). We herein discuss three models, which differ significantly in the timescale they predict. These include: (1) the CTF expanded in response to increased ecological opportunities after extinction of the ETB and/or in response to the environmental changes that supposedly caused this extinction; (2) the extinction of the ETB was the endpoint of a long-term demise due to competition with the expanding CTF; (3) the end-Ediacaran mass extinction reflects the tipping point at which the development of mobility allowed the acquisition of new feeding strategies in the CTF, negatively affecting the ETB by the destruction of the vital microbial matground food source or by direct interference (e.g. predation).

The first model predicts that the expansion of the CTF began *after* the onset of the hypothesized changes in environmental conditions (Fig. 7a). However, it is unlikely that the short duration of the ECTI, as benchmarked by our new age data, was sufficient for a *de novo* evolution of the morphological complexity of Cambrian trace-makers with its advanced grade of organization comparable to that of priapulid worms (Vannier et al., 2010). The second model, which conforms to Benton's metaphoric 'double wedge' (Benton, 1987; Sepkoski, 1996), predicts an extended period of replacement, during which the CTF expanded at the expense of the ETB (Fig. 7b). The diversity

decline from the older White Sea assemblages to the younger Nama assemblages has been depicted in this light (Darroch et al., 2015; Muscente et al., 2018), as have the sporadic reports of rangeomorphs from the Cambrian (Jensen et al., 1998; Hagadorn et al., 2000). However, survivorship of rangeomorphs into the Cambrian is questionable (Laflamme et al., 2013) and represents at best an exception. Generally, rangeomorphs are not found above the lowest occurrence of Cambrian trace-makers, and there is no evidence for a successive decline during an extended period of co-existence in Namibia, or globally.

It has frequently been proposed that the extinction of the ETB was ecologically driven, e.g. by destruction of the matground environment by newly evolved sediment-mixing metazoans, competition with ecologically more successful animals, or predation (Bengtson and Yue, 1992; Seilacher and Pflüger, 1994; Schiffbauer et al., 2016). Ecological effects of newly evolved key adaptations that enhanced competitiveness, predatory skills or the ability to alter the habitat would appear geologically suddenly, analogous at a larger scale to the profound alterations of some present-day ecosystems following the introduction of invasive species (Lowe et al., 2004). We suggest that an adaptive breakthrough, such as the evolution of advanced mobility, could shift the process of clade replacement from the evolutionary to the ecological timescale, leading to a situation that is herein referred to as the *truncated double wedge model* (Fig. 7c): one clade declines progressively in response to the expansion of another until an adaptive breakthrough accelerates this replacement by orders of magnitude, leading to the truncation of the shrinking 'wedge'. The progressive decline of the rangeomorphs/erniettomorphs during the late Ediacaran, contrasted by the short interval of their final disappearance benchmarked by the new age data, is predicted by this model. A possible preservation bias against ETB in the Cambrian (Gehling, 1999) may have accentuated the abruptness of this transition. However, the persistence of microbial mats into the basal Cambrian, and uncertainties in the taxonomic identity of potential Cambrian rangeomorphs/erniettomorphs, casts the empirical evidence for this model into doubt (Laflamme et al., 2013).

Summarized, we found the best model-to-data fit for the truncated double wedge model, although our data are not completely incompatible with an environmentally driven scenario, at least if (1) the maximum duration within the error of the age data is assumed and (2) the geologic time represented by the erosional unconformity was short. However, evidence for possible environmental changes is currently weak, which also detracts from a possible scenario in which environmental and evolutionary aspects worked in concert during the Ediacaran–Cambrian biotic transition.

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FIGURE CAPTIONS

Figure 1. Geological map of southern Namibia and the Nama basin (Grotzinger and Miller, 2008).

Figure 2. Geological map of the farms Swartkloof, Swartpunt and Nord-Witpütz. Note location of the Swartpunt section (units A–F) and the Swartkloofberg section (unit G) (modified from Saylor and Grotzinger, 1996).

Figure 3. Geologic sections at Swartpunt (units A–F) and Swartkloofberg (unit G) indicating the Ediacaran–Cambrian boundary interval in the Swartpunt and Swartkloofberg sections. Precise U–Pb ages obtained by CA-ID-TIMS techniques with uncertainties given at 2 sigma level, carbon isotope values and fossil horizons. 1 – debris flow, shale, olistoliths; 2 – shale, sandstone, conglomerate; 3 – grey-green sandstone, 4 – greenish shale; 5 – grey thick-bedded micrite; 6 – grey thin-bedded micrite; 7 – black thick-bedded micrite; 8 – black thin-bedded micrite; 9 – ash bed.

Figure 4. Fossils from the Swartpunt and Swartkloofberg sections. A – *Pteridinium simplex* Gürich, 1930; Spitskop Member, unit D, metre 104. B – *Streptichnus narbonnei* Jensen and Runnegar, 2005; Spitskop Member, unit F, metre 126. C – Unusually small specimen assigned to *Streptichnus*

narbonnei Jensen and Runnegar, 2005; Spitskop Member, unit F meter 127. D – *Treptichnus* cf. *pedum* (Seilacher, 1955), garlands crossing each other; Spitskop Member, unit F, meter 127. E – Incompletely preserved vertical burrows resembling *Bergaueria*; unit F meter 127. F – Branched traces with secondary weak mineralization of outer surface (arrows point to branching points), tentatively assigned to *Olenichnus*; Spitskop Member, unit F, metre 127. G – Shallow horizontal burrows with different types of annulations (arrows) suggesting a spiral burrow; Spitskop Member, unit F, metre 127. H – *Cochlichnus* isp.; from Nomtsas Formation, unit G. I – Trace fossil assemblage with simple *Planolites*-type horizontal traces crossing each other, associated with a string-of-pearl-type or pelleted trace (arrow in lower left corner) and delicate traces composed of elongate probes (arrow near right margin); Nomtsas Formation, unit G above ash 6. J – Irregularly sinuous pelleted trace with subregular constrictions; Nomtsas Formation, unit G. White scale bars (in B, D, E, G, H, J) equal 5 mm, black scale bars (in C, F) 5 mm. Coin diameter 22.6 mm (in A, I).

Figure 5. Concordia diagrams of the CA-ID-TIMS U-Pb zircon data (for position of ashes in the section see Figs. 3 and 6).

Figure 6. Range of life forms and suggested biological developments versus age including new geochronological data (this study) in a time window ranging from 540.1 to 538.3 Ma indicating the Ediacaran–Cambrian boundary interval in the Swartpunt and Swartkloofberg sections.

Figure 7. Three models for the displacement of the Ediacara-type biota (ETB, blue) by the Cambrian-type fauna (CTF, red); x-axis represents diversity; shaded interval indicates hypothetical environmental disturbances in (a).